

# Tsetse Fly Population Outcomes for a Number of Aerial Spray Scenarios at Different Temperatures

S. J. Childs

SACEMA, University of Stellenbosch

Stellenbosch, 7600, South Africa

tel: (+27/0) 21 8082589, email: schilds@sun.ac.za,

2008

## Abstract

*The hypothetical impact of aerial spraying strategies on tsetse fly is investigated. The investigation is largely one of the effect of temperature on tsetse population dynamics and its reproductive cycle during spraying, given that cooler weather is preferred for the settling of insecticidal droplets. Conventional insecticidal spraying strategies are found to be more costly in cooler weather because of the greater number of required cycles. This is due to the larger ratios of puparial duration versus first interlarval period implied by lower temperatures. The conventional strategy consequently requires a far greater number of spray cycles at lower temperature.*

*Pupae, which are the immediate descendants of pre-spray-existing pupae (and not third generation, or higher, pupae), are identified as the main threat to successful control by aerial spraying. Costs and physical reasons aside, the investigation determines that there is little difference between the outcomes of the conventional strategy at different temperatures. Given such high kill rates, it is not surprising that the outcome is largely determined by the size of the emergent population which were only subjected to the last two sprays.*

Keywords: Tsetse; glossina morsitans; Westwood; aerial spraying; insecticide; deltamethrin; trypanosomiasis; sleeping sickness; diptera; glossinidae.

## 1 Introduction

The reproductive life cycle of the tsetse fly is particularly well disposed to control through the periodic application of insecticide. This is since it is both highly structured and steady, for a

given temperature, and it is in this that there lies a major vulnerability open to exploitation for their control. Conventional insecticidal spraying strategies for tsetse entail scheduling spray cycles two days short of the first interlarval period and stopping only once two sprays subsequent to the emergence of the last pre-spray pupae (one puparial duration) have been carried out.

The hypothetical impact of these strategies is investigated in this work. Conventional tsetse spraying strategies are found to be more costly in cooler weather. This is due to the larger ratios of puparial duration versus first interlarval period implied by lower temperatures. The conventional strategy consequently requires a far greater number of spray cycles at lower temperature.

A brief overview of the reproductive life cycle of the tsetse fly is given and the conventional strategy for the aerial application of insecticide is outlined. Although the resulting model itself is capable of accepting variable temperature inputs, results are presented in terms of constant temperature; for obvious reasons. (An assumption of constant temperature for the duration of spraying would, however, not be that unreasonable if one considers the variation in temperature presented in HARGROVE [1].)

For the purposes of understanding, the problem is also expounded in terms of a number of formulae: A formula for the survival of original, pre-spray-existing, adult females, a formula for the survival of pre-spray-existing pupae, a formula for the production and survival of the immediate off-spring of both these categories and, finally, a formula for the production and survival of third generation and higher flies. The model itself is capable of accepting variable temperature inputs although the results are presented in terms of constant temperature.

Surviving flies themselves are of no real consequence to the outcome of a spraying operation. Second generation pupae which are the immediate descendants of pre-spray-existing pupae (and not third generation, or higher, pupae) are the main threat to success.

## 2 Life Cycle of the Tsetse Fly

The reproductive life cycle of the tsetse fly is steady for a given temperature and it is in this that there lies a major vulnerability open to exploitation for their control. The population dynamics are largely temperature and age dependent in the short term (HARGROVE [1] and [2]) and variables such as humidity and vegetation index are thought to be relevant only in the medium to long term.

Pupae are deposited in the ground where they remain for a period of time,  $\tau_0$ , the puparial duration. The puparial duration is a function of temperature,  $T$ . Pupae also die off at some daily rate,  $e^{-\delta_0(T)}$ , and the tsetse flies which subsequently emerge have a probability  $\gamma$  of being female.

During the first few hours, the young, teneral fly's exoskeleton is soft and pliable, its fat reserves are at their lowest and a first blood meal is imperative for survival. It is at this time that the

insect is at its most vulnerable and it is also at this time that it is at its most dangerous to humans. The tsetse mortality rate,  $e^{-\delta(t,T)}$ , can be approximated as  $e^{-\delta_1(T)t}$  at this early stage of the life cycle, the time between female eclosion and ovulation ( $t$  denotes age, for the present). Thereafter the female tsetse fly's mortality rate can be approximated as  $e^{-\delta_2(T)t}$ .

The female tsetse fly mates only once in her life with the chance  $\eta$  that she is successfully inseminated. The time between female eclosion and the production of the first pupae is known as the first interlarval period,  $\tau_1(T)$ . Thereafter she produces pupae at a shorter interlarval period,  $\tau_2(T)$ .

The accumulated mortality rate is therefore

$$\delta(t, T) = \begin{cases} \delta_1(T)t & \text{for } t < \tau_1 - \tau_2 \\ \delta_2(T)(t - [\tau_1(T) - \tau_2(T)]) + \delta_1(T) [\tau_1(T) - \tau_2(T)] & \text{for } t \geq \tau_1 - \tau_2. \end{cases}$$

The puparial duration is

$$\tau_0 = \frac{1 + e^{a+bT}}{k},$$

where  $k = 0.057 \pm 0.001$ ,  $a = 5.5$  and  $b = -0.25$  (PHELPS AND BURROWS [13] and HARGROVE [6]). The time taken from female eclosion to the production of the first pupa is

$$\tau_1 = \frac{1}{k_1 + k_2(T - 24)},$$

where  $k_1 = 0.061$  and  $k_2 = 0.0020$  (HARGROVE [3] and HARGROVE [4]). The subsequent interlarval period is

$$\tau_2 = \frac{1}{k_1 + k_2(T - 24)},$$

where  $k_1 = 0.1046$  and  $k_2 = 0.0052$  (HARGROVE [3] and HARGROVE [4]). Some maximum possible birth rate,  $\beta$ , for a population in equilibrium is assumed. Table 1 lists some values of the aforementioned parameters at different temperatures.

	16°C	18°C	20°C	22°C	24°C	26°C	28°C	30°C
$\beta$	0.0094	0.0120	0.0146	0.0173	0.0197	0.0220	0.0241	0.0259
$\delta_0$	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
$\delta_1$	0.0188	0.0240	0.0293	0.0345	0.0395	0.0440	0.0481	0.0519
$\delta_2$	0.0094	0.0120	0.0146	0.0173	0.0197	0.0220	0.0241	0.0259

Table 1: Parameters at different temperatures.

### 3 Strategy for the Aerial Application of Insecticide

The reproductive life cycle of the tsetse fly is particularly well disposed to control through the periodic application of insecticide. The aerial application of small amounts of deltamethrin can be expected to be so effective as to produce a 99.9% mortality in the fly population. Pupae present in the ground during spraying are, however, unaffected by the insecticide. The idea is therefore to schedule follow-up operations shortly before the first flies to emerge from pupae, after spraying, themselves mature and lay eggs. Subsequent sprays are consequently scheduled two days short of the interlarval period, in other words,

$$\sigma = \tau_1 - 2, \quad (1)$$

where  $\sigma$  is the interval between spray cycles. Spray cycles should be repeated until the last pre-spray-existing pupae emerge from the ground. The conventionally accepted strategy advocates spray cycles continue until at least two sprays after the emergence of the last flies from pre-spray-existing pupae. That is,

$$(s - 1)\sigma - \sigma > \tau_0, \quad (2)$$

where  $s$  is the total number of cycles. Table 2 lists the values of  $\sigma$  at different temperatures.

	16°C	18°C	20°C	22°C	24°C	26°C	28°C	30°C
$\sigma$	20	18	17	16	14	13	12	12

Table 2: The length of a cycle,  $\sigma$ , at different temperatures.

Substituting equation 1 into equation 2 yields

$$s > \frac{\tau_0}{\tau_1 - 2} + 2.$$

At this early juncture it is worth noting that, at lower temperatures, the required number of spray cycles is high, whereas at higher temperatures, the required number of spray cycles is low. Although the combined values of  $\beta$  (the maximum possible growth rate in table 1) and  $\tau_0$  give rise to a greater number of pre-spray-existing pupae at low temperature, it is the relative values of  $\tau_0$  and  $\sigma$  which ultimately compromises spraying at low temperature. Spraying at high temperature is more difficult in practice as a result of the fine insecticide droplets failing to settle in warm air, which rises.

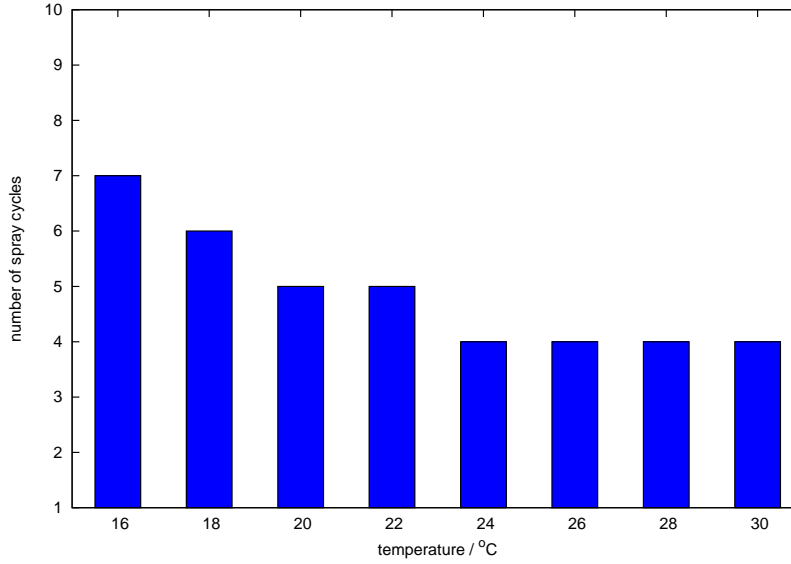


Figure 1: The minimum number of spray cycles,  $s$ , required at different temperatures.

## 4 Population Performance During Spraying

The state of the population at the completion of spraying is, for the purposes of this discussion, considered in the context of three categories: Original, pre-spray-existing adults; original, pre-spray-existing pupae; inter-spray pupae. Although such an analysis is not necessary for algorithmic purposes it is helpful from the point of view of understanding.

### 4.1 Survival Of Original, Pre-Spray-Existing Adults

The number of surviving, female members of the original population, at the conclusion of spraying, is

$$N e^{-\delta_2(T)(s-1)\sigma} \phi^s, \quad (3)$$

where  $N$  is the original, steady-state, equilibrium number of females prior to spraying,  $\delta_2(T)$  is the worst-case-scenario mortality rate (that for mature adults)<sup>1</sup>,  $\phi$  is the spray survival factor for a single spray cycle and  $s$  is the number of spray cycles.

---

<sup>1</sup>no age distribution profile has been assumed for simplicity

## 4.2 Survival Of Pre–Spray–Existing Pupae

Pupae present in the ground during spraying are unaffected by the insecticide. The total number of spray cycles the flies emergent from such pupae are subsequently subjected to is therefore determined by their day of emergence. The total number of insecticidal spraying cycles the flies are subjected to is

$$\text{floor} \left\{ \frac{\sigma(s-1) - \check{t}}{\sigma} \right\} + 1,$$

where  $\text{floor}\{\cdot\}$  is the least integer function and  $\check{t}$  is the time from the first spray cycle to the flies' emergence. The newly emergent flies subsequently also die off at some age-dependent rate. The number of surviving female flies, at some later time,  $t$ , is therefore

$$\sum_{\check{t}=1}^{\tau_0(T)} \gamma E_{\text{pre-spray}} e^{-\delta(t-\check{t},T)} \phi^{\text{floor}\left\{\frac{\sigma(s-1)-\check{t}}{\sigma}\right\}+1},$$

where  $E_{\text{pre-spray}}(\check{t})$  is the number of flies emergent at time  $\check{t}$ .

Setting  $t = (s-1)\sigma$  i.e. the last spray and taking cognisance of the fact that the number of flies emergent from existing pre-spray pupae is assumed constant for a population which was at a steady state and constant temperature prior to the commencement of spraying, yields

$$\gamma E_{\text{pre-spray}} \left[ \sum_{\check{t}=1}^{\tau_0(T)} e^{-\delta((s-1)\sigma-\check{t},T)} \phi^{\text{floor}\left\{\frac{\sigma(s-1)-\check{t}}{\sigma}\right\}+1} \right], \quad (4)$$

where  $e^{-\delta(t,T)}$  is the previously described mortality,

$$E_{\text{pre-spray}} = \gamma\beta N,$$

$N$  is the equilibrium number of adult females prior to the commencement of spraying and  $\beta$  is the steady-state, maximum, possible, female birth (eclosion) rate (see WILLAITS, DRANSFIELD and BRIGHTWELL [16]).

## 4.3 Production and Survival of Inter–Spray Pupae

The survival of flies emergent from inter-spray pupae can be deduced by similar reasoning to the aforementioned case, the exception being that the number of emergent flies is not constant over time. The number of such flies after the last spray is

$$\sum_{\check{t}=\tau_0(T)+1}^{\sigma(s-1)} \gamma E(\check{t}) e^{-\delta((s-1)\sigma-\check{t},T)} \phi^{\text{floor}\left\{\frac{\sigma(s-1)-\check{t}}{\sigma}\right\}+1}. \quad (5)$$

Contributions to  $E(\check{t})$  arise, in this case, as a result of flies emergent from pupae deposited  $\check{t} - \tau_0$  days before. The pupae were deposited by one of the aforementioned, two survival or interspray pupae categories, themselves.

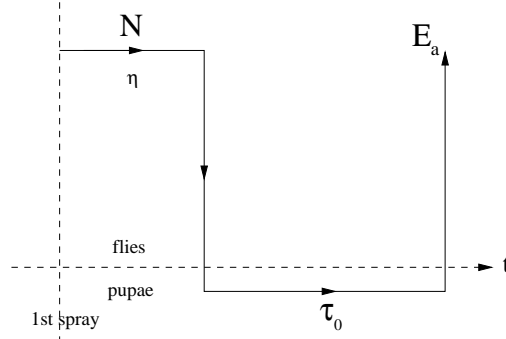


Figure 2: Second generation flies emerging from inter-spray pupae that are descended from surviving, pre-spray adults.

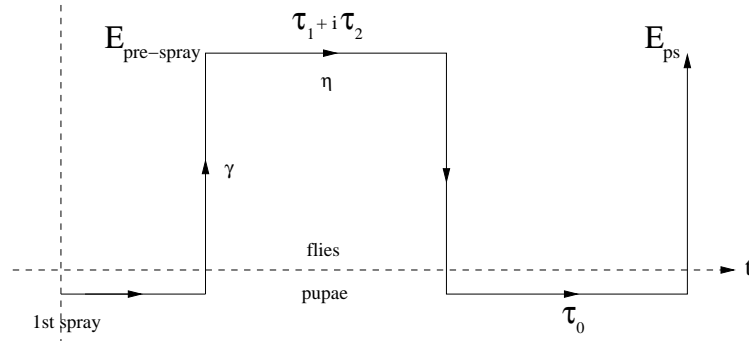


Figure 3: Second generation flies emerging from inter-spray pupae that are descended from pre-spray-existing pupae.<sup>1</sup>

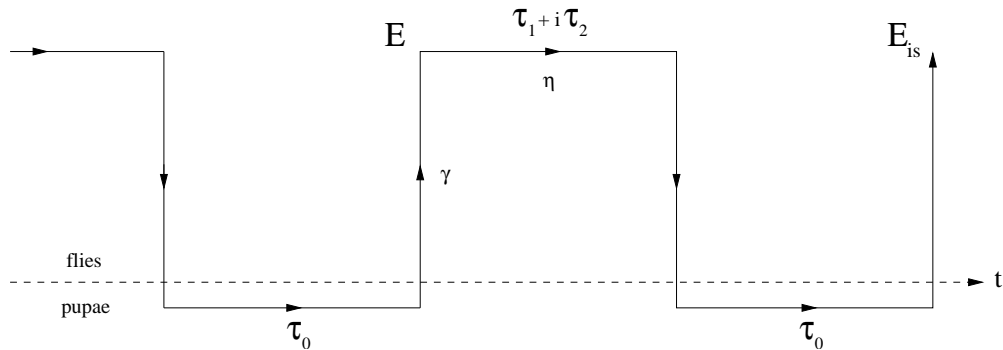
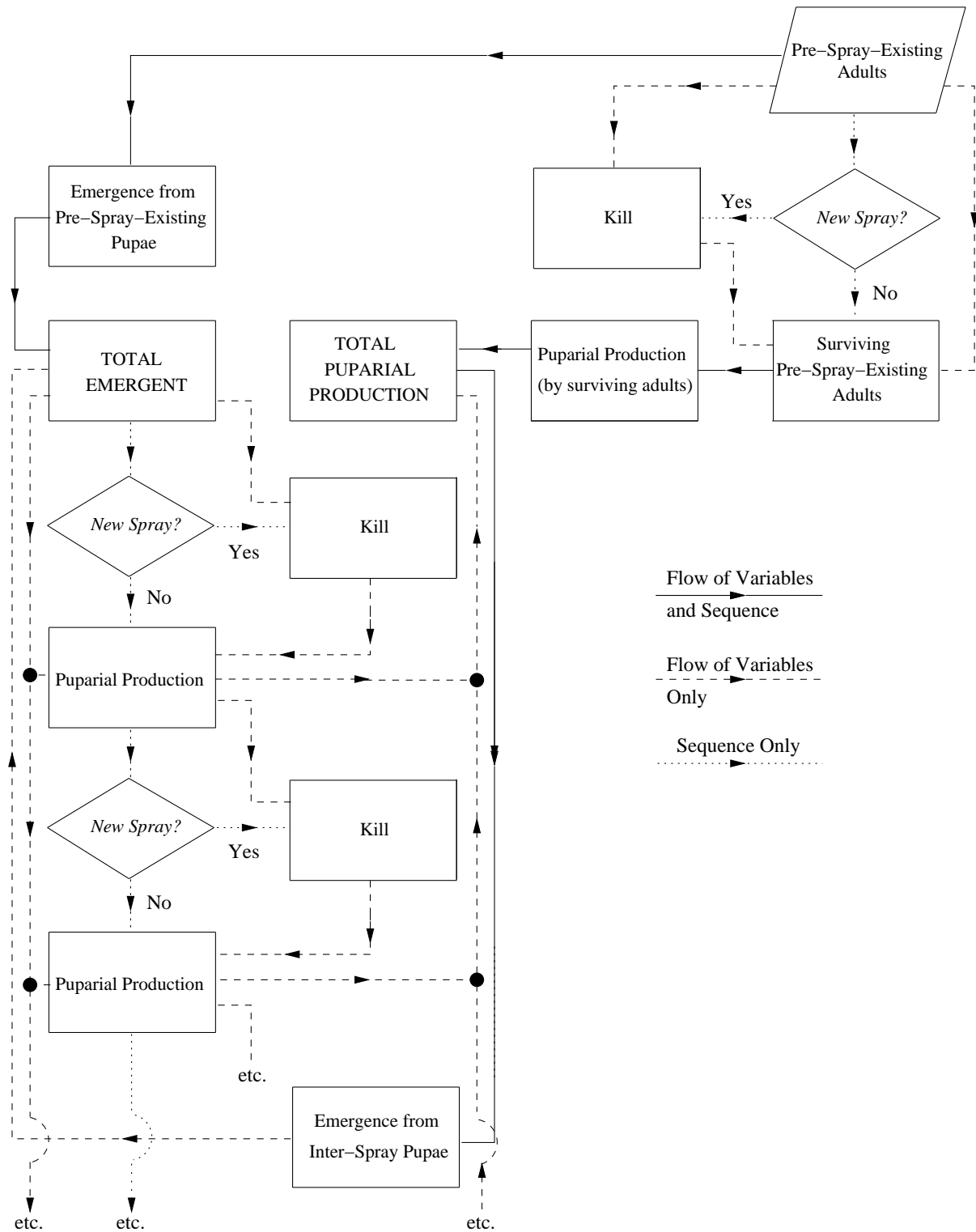


Figure 4: Flies emerging from inter-spray pupae that are descended from inter-spray pupae themselves (third generation and higher).<sup>1</sup>

Figure 5: Flow chart of the computation for a generalised day  $i$ .

<sup>1</sup> $\tau_2$ , hence temperature, assumed constant for simplicity.

### Contributions to $E(\check{t})$ by Original, Surviving, Pre–Spray Adults

An obvious prerequisite for such contributions to a second generation is that  $\check{t} > \tau_0$ . This fact is clearly illustrated in the schematic diagram, Figure 2 (on page 7). The worst–case–scenario mortality rate<sup>1</sup> (that for mature adults) is again assumed, consistent with equation 3.

$$E_a(\check{t}) = \eta \frac{N}{\tau_2} e^{-\delta_2(\check{t}-\tau_0)-\delta_0\tau_0} \phi^{\text{floor}\left\{\frac{\check{t}-\tau_0}{\sigma}\right\}+1}. \quad (6)$$

### Contributions to $E(\check{t})$ by Female Flies from Pre–Spray–Existing Pupae

The first and most obvious requirement for such second generation decendance is that  $\check{t} > \tau_0 + \tau_1$ . This fact is clearly illustrated in the schematic diagram, Figure 3 (on page 7). Secondly, only for a limited period of time (the puparial duration) do flies from pre–spray–existing pupae continue to emerge from the ground. That is

$$\begin{aligned} 1 \leq \check{t} - \tau_0 - \tau_1 - i\tau_2 \leq \tau_0 \quad i = 0, 1, \dots \\ \max \left\{ 0, \text{ceiling} \left\{ \frac{1}{\tau_2} (\check{t} - 2\tau_0 - \tau_1) \right\} \right\} \leq i \leq \frac{1}{\tau_2} (\check{t} - \tau_0 - \tau_1 - 1). \end{aligned}$$

Adapting equation 4

$$\begin{aligned} E_{ps}(\check{t}) = E_{\text{pre-spray}} \sum_{i=\max\left\{0, \text{ceiling}\left\{\frac{1}{\tau_2}(\check{t}-2\tau_0-\tau_1)\right\}\right\}}^{\text{floor}\left\{\frac{1}{\tau_2}(\check{t}-\tau_0-\tau_1-1)\right\}} \left[ \gamma \eta e^{-\delta(\tau_1+i\tau_2)-\delta_0\tau_0} \right. \\ \left. \phi^{\left(\text{floor}\left\{\frac{\check{t}-\tau_0}{\sigma}\right\}-\text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2}{\sigma}\right\}\right)} \right]. \quad (7) \end{aligned}$$

[Note that  $\tau_0(T)$  and  $\tau_2(T)$ , hence the temperature on which they depend, have been assumed constant in the above formula. It should be stressed that no such constant temperature assumption needs to be made during computation. Constant temperature is the context in which the results to follow were generated.]

### Contributions to $E(\check{t})$ by Female Flies Descended from Inter–Spray Pupae Themselves

The first prerequisite for such third, or greater, generation contributions is that  $\check{t} > 2\tau_0 + \tau_1$ . This fact is clearly illustrated in the schematic diagram, Figure 4 (on page 7). Secondly, since inter–spray pupae only begin to emerge at time  $\tau_0 + 1$ , (just when the pre–spray pupae cease to

<sup>1</sup>no age distribution profile has been assumed for simplicity

emerge)

$$\begin{aligned} \tau_0 + 1 &\leq \check{t} - \tau_0 - \tau_1 - i\tau_2 \leq \check{t} & i = 0, 1, \dots \\ \max \left\{ 0, \text{ceiling} \left\{ \frac{1}{\tau_2}(-\tau_0 - \tau_1) \right\} \right\} &\leq i \leq \frac{1}{\tau_2}(\check{t} - 2\tau_0 - \tau_1 - 1) \\ 0 &\leq i \leq \text{floor} \left\{ \frac{1}{\tau_2}(\check{t} - 2\tau_0 - \tau_1 - 1) \right\}. \end{aligned}$$

Adapting equation 5 and taking cognizance of the fact that the number of emergent flies is not constant over time under such circumstances,

$$\begin{aligned} E_{is}(\check{t}) = & \sum_{i=0}^{\text{floor}\left\{\frac{1}{\tau_2}(\check{t}-2\tau_0-\tau_1-1)\right\}} \left[ \gamma \eta E(\check{t} - \tau_0 - \tau_1 - i\tau_2) \right. \\ & \left. e^{-\delta_2(\tau_1+i\tau_2)-\delta_0\tau_0} \phi\left(\text{floor}\left\{\frac{\check{t}-\tau_0}{\sigma}\right\} - \text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2}{\sigma}\right\}\right) \right]. \end{aligned} \quad (8)$$

From this point on the origins of the inter-spray pupae are no longer relevant and generations higher than the third are accounted for through recursion.

[Note that  $\tau_0(T)$  and  $\tau_2(T)$ , hence the temperature on which they depend, have been assumed constant in the above formula. It should be stressed that no such constant-temperature assumption needs to be made during computation. Constant temperature is the context in which the results to follow were generated.]

## 5 Female Pupae which will Survive Spraying

The number of female pupae remaining in the ground at the end of spraying and **which will survive to emerge**, is

$$\sum_{\check{t}=\sigma(s-1)+1}^{\sigma(s-1)+\tau_0(T)} \gamma E(\check{t}) e^{-\delta_0\tau_0}. \quad (9)$$

Contributions to  $E(\check{t})$  arise as a result of flies emergent from pupae deposited  $\check{t} - \tau_0$  days before. The pupae were deposited by one of the aforementioned categories.

## 6 Results

Surviving flies and pupae from a starting fly population of  $8 \times 10^6$  are presented in Figures 6 through to 8. The results were generated for a range of constant temperatures. The daily temperature variation presented in HARGROVE [1] suggests real-life scenarios in which mean daily temperature varies little.

Note that surviving flies themselves are of no real consequence to the outcome of a spraying operation. In fact no female tsetse flies, at all, survive a kill rate of 99.99%.

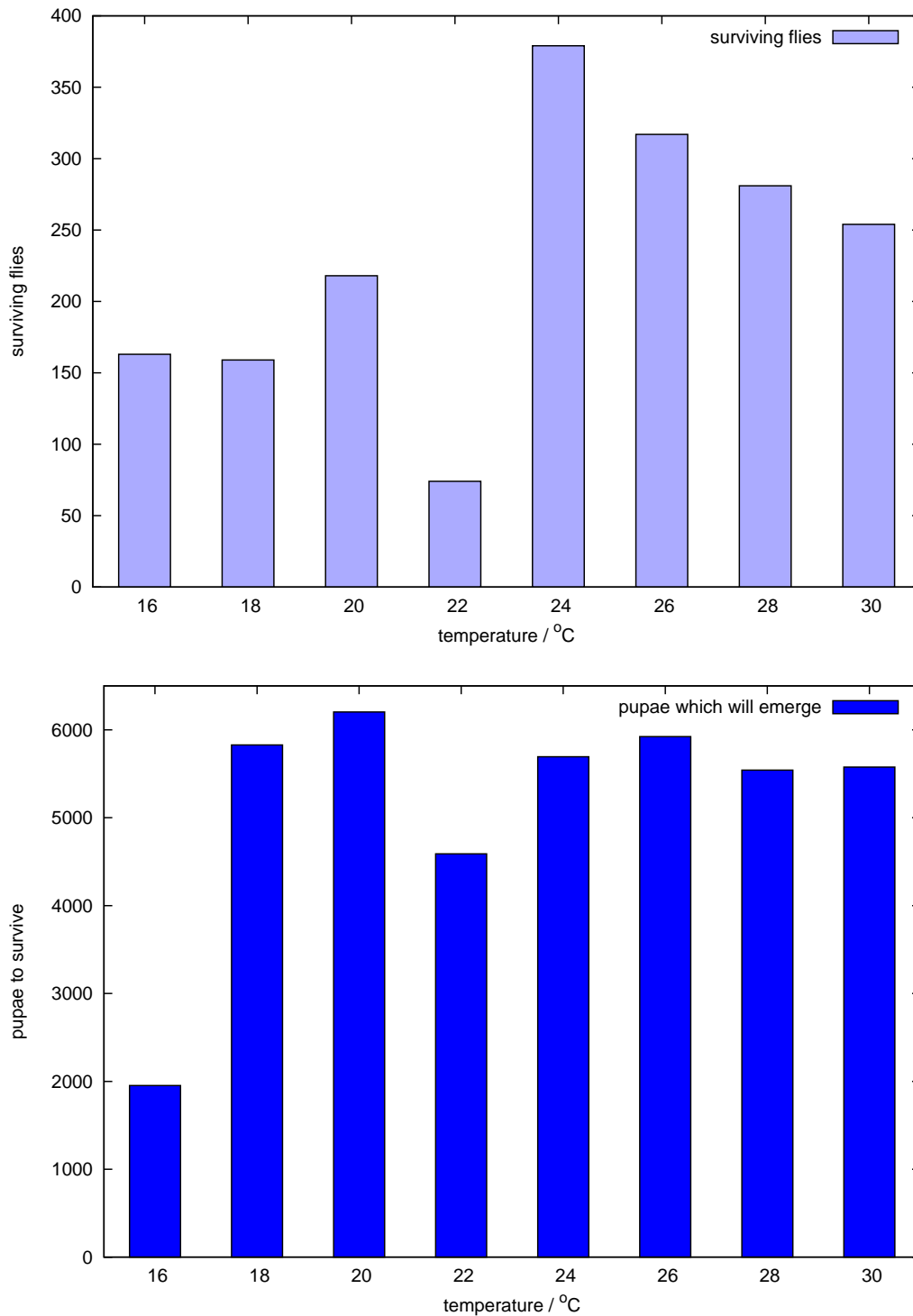


Figure 6: Number of female tsetse flies and female pupae (which will survive to emerge) at the end of spraying, given a low kill rate of 99%.

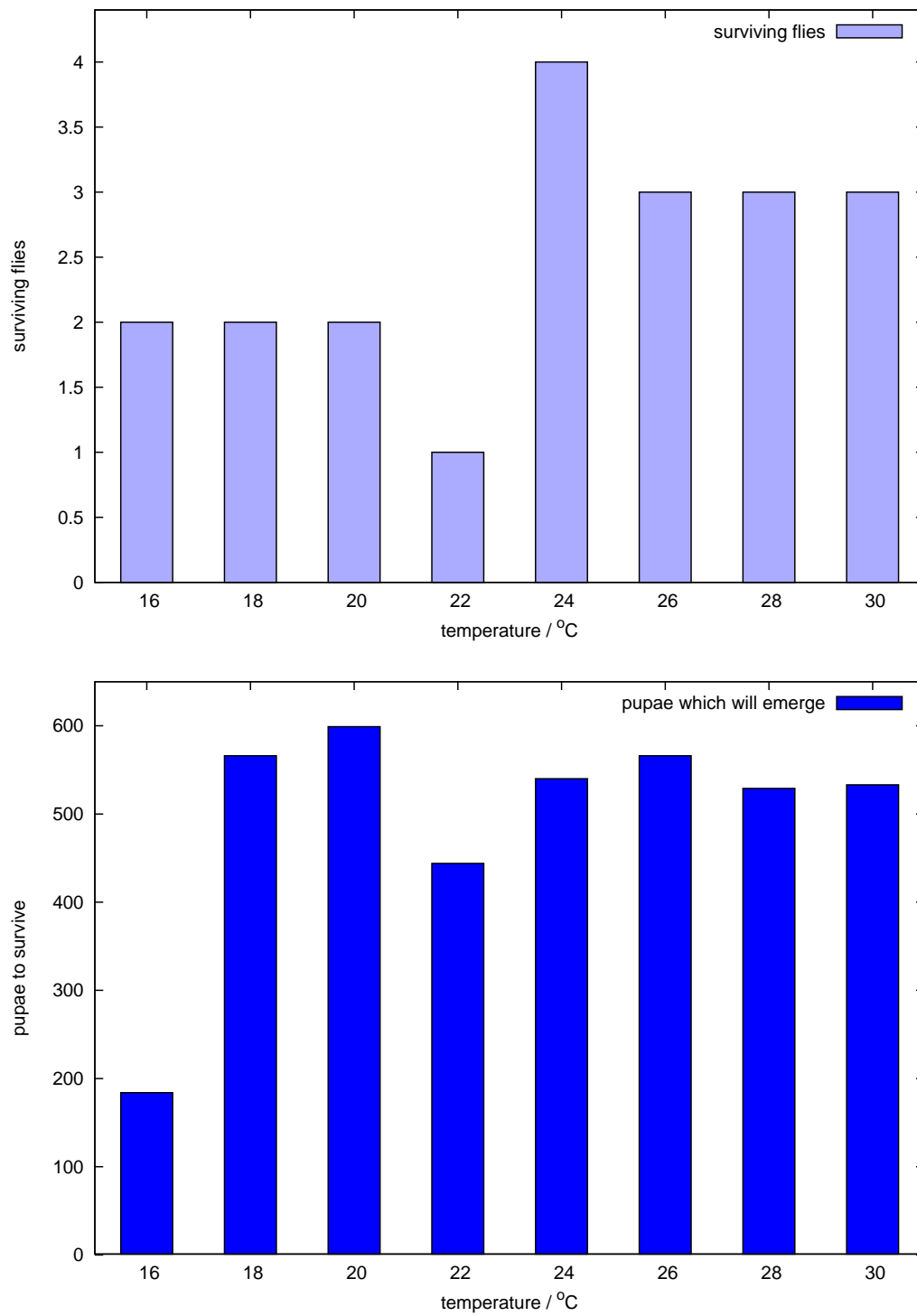


Figure 7: Number of female tsetse flies and female pupae (which will survive to emerge) at the end of spraying, given a kill rate of 99.9%.

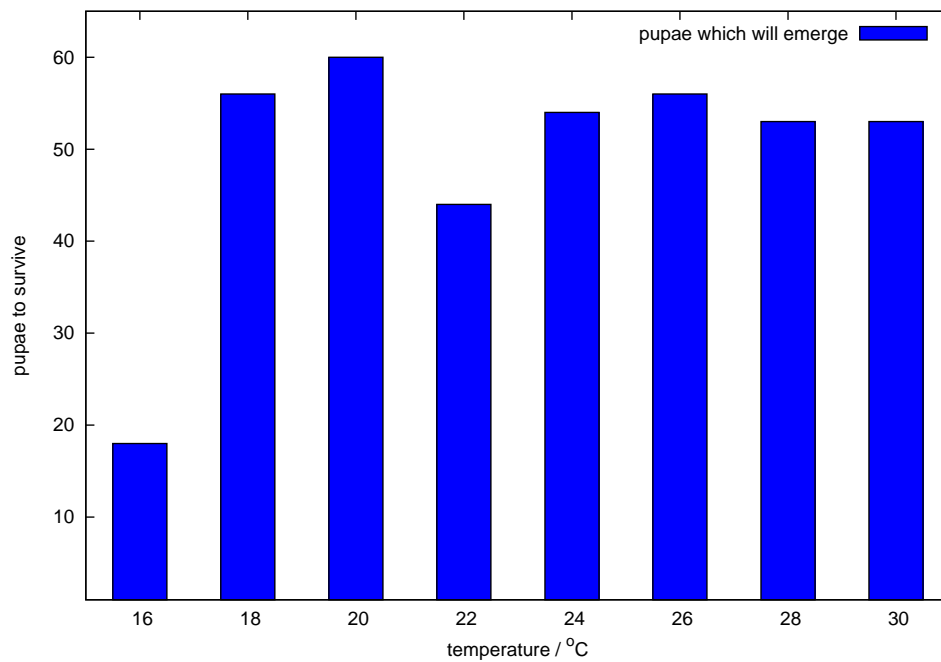


Figure 8: Number of female pupae which will survive to emerge at the end of spraying, given a high kill rate of 99.99%. No female tsetse flies survive.

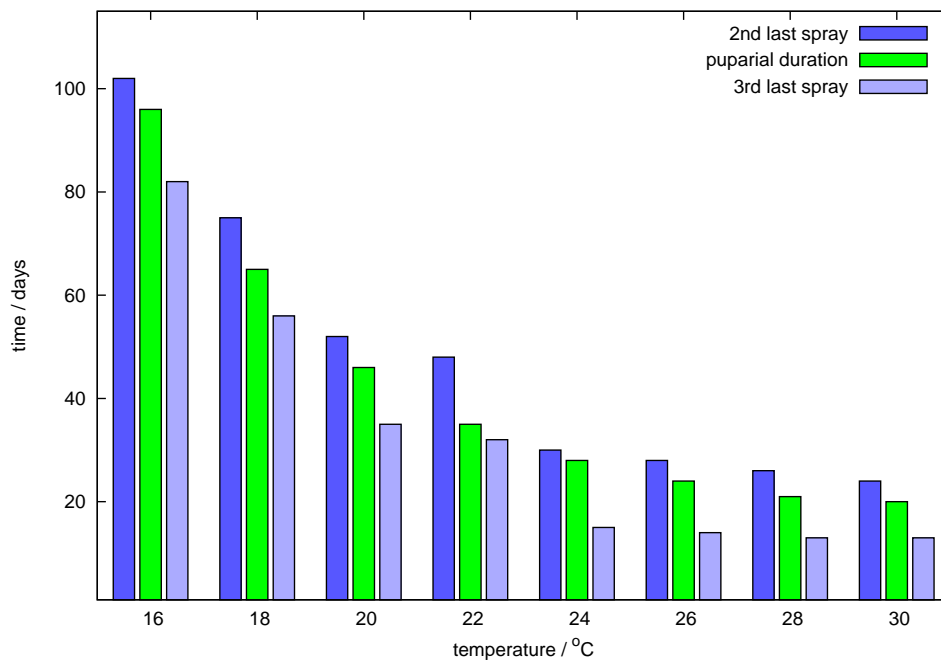


Figure 9: Explanation of the results: At such high kill rates the primary influence on the outcome is the number of emerging, pre-spray pupae which are only subjected to two sprays.

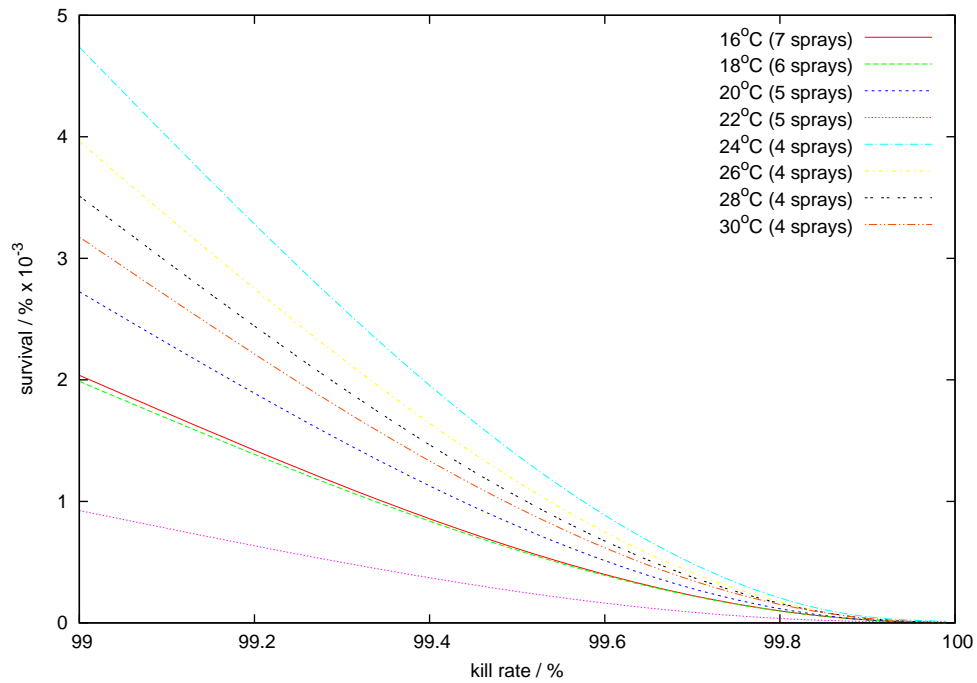


Figure 10: Remaining female fly population. The difference in outcomes is small.

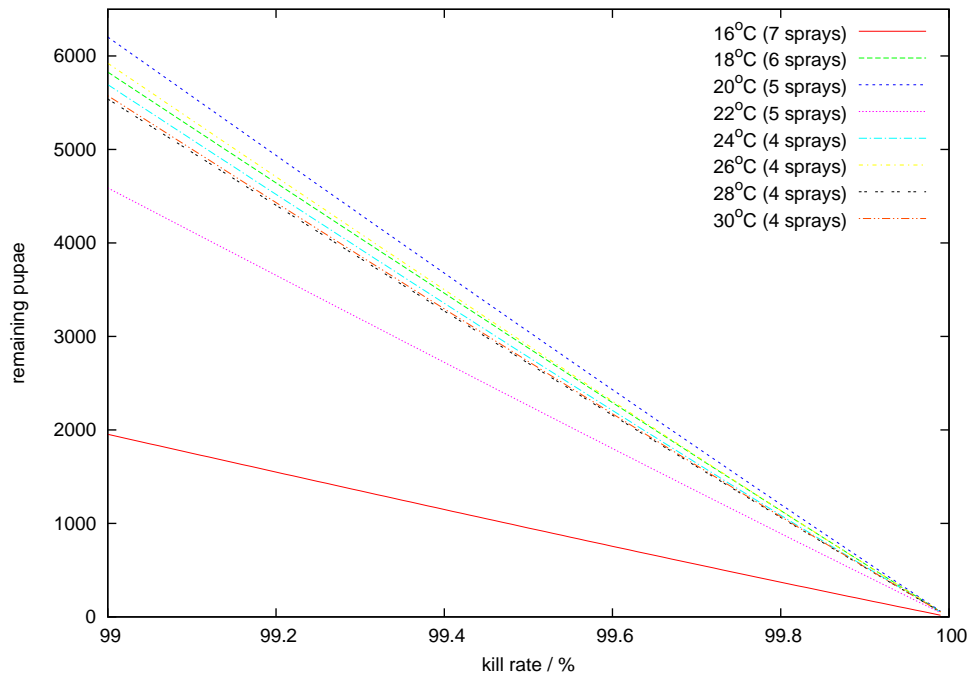


Figure 11: The number of female pupae still in the ground, given a starting population of  $8 \times 10^6$  adult flies in equilibrium with the the quoted temperature.

## 6.1 The Origins of the Pupae Still to Emerge

Figure 12 presents a compositional analysis of the origins of female pupae still in the ground at the end of spraying and which will emerge. Dominance by the daughters-of-pre-spray-pupae category at higher kill rates becomes absolute.

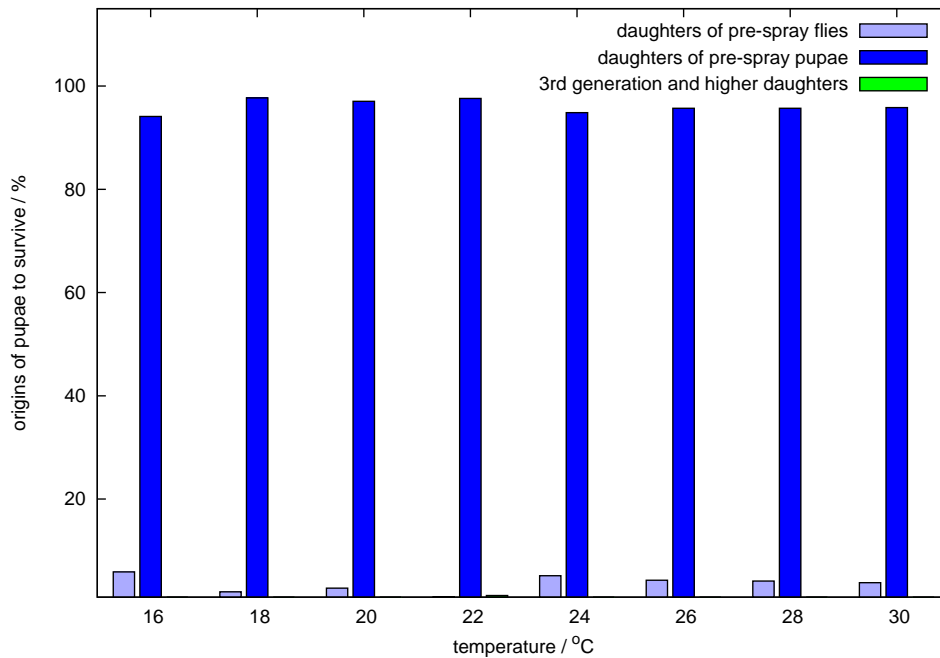


Figure 12: The origins of the female pupae still in the ground at the end of spraying given a low kill rate of 99%. Dominance by the daughters-of-pre-spray-pupae category at higher kill rates becomes absolute.

Note that although the values of  $\beta$  (the maximum possible growth rate) give rise to a greater number of pre-spray-existing pupae at low temperature, it is the relative values of  $\tau_0$  and  $\sigma$  which ultimately have the most profound consequences for spraying at low temperature.

## 7 The Ethics and Environmental Impact of Spraying

Maximum doses of  $0.26 gha^{-1}$  to  $0.3 gha^{-1}$  deltamethrin were used in the land mark operation described by KGORI, MODO AND TORR [9]. It is claimed that such doses have no, to little, residual effect. NAGEL [11] nonetheless points out that care needs to be taken with deltamethrin near shell fisheries and other crustaceans. No conclusion is reached with regard to apiaries or subsequent effects on the pollination of crops, although honey bees certainly are killed by the insecticide (NAGEL [11]).

Flight emergencies do happen and cattle died as a result of one such incident where the insecticidal load had to be dumped in Zambia. Although NAGEL [11] attributes these deaths to a mismanaged response and non-compliance with subsequent advice, rather than the insecticidal operation itself, it should be remembered that aerial spraying is usually carried out in remote areas where there are often problems in communication and levels of education are sometimes poor.

Some would argue that NAGEL [11] does not go far enough. They would argue that work, such as that by PERKINS and RAMBERG [12], suggests that a full 10% of known species of shrimps and back-swimmers are permanently lost as a result of aerial spraying. They would argue in favour of more discriminate means of control, such as pour-ons and targets. They would also claim that if people are prepared to entertain concepts such as S.I.T. (sterile insect technique), a bio-control programme utilising the tsetse flies' natural enemies is an option which also warrants investigation.

There are some environmentalists who would go so far as to claim that the tsetse fly has a unique role in shaping a large number of African environments and shouldn't be eradicated. They would argue that the now extinct Cape quagga was merely a common zebra whose habitat had long been separated from that of the tsetse fly and that many species, such as the wild dog, would otherwise already be extinct. They would claim that in the many areas where there is no human trypanosomiasis e.g. South Africa, inoculation of livestock works, furthermore, that there is an even simpler solution; notably game farming. LEAK [10] provides a grim reminder that in the opening years of the previous century, around 200 000 people died of trypanosomiasis in the provinces of Buganda and Busoga alone and that these provinces eventually had to be evacuated.

## 8 Conclusions

Costs and physical reasons aside, this investigation determines that there is little difference between the outcomes of the conventional strategy at different temperatures. Given such high kill rates, it is not surprising that the primary influence on the results is the difference in time between the third last spray and the end of one puparial duration. The outcome is largely determined by the size of the population which were subjected to only two sprays. At 22°C, for example, only a very small fraction of the emerging pre-spray pupae are subjected to only two sprays.

The issue of a more expensive spraying operation at low temperature, due to a greater, required number of spray cycles needs to be considered. Conventional insecticidal spraying strategies are found to be more costly in the cooler weather preferred for the settling of insecticidal droplets. This is due to the larger ratios of puparial duration versus first interlarval period implied by lower temperatures. The conventional strategy consequently requires a far greater number of spray cycles at lower temperature. Comparison is further complicated by the fact that the same equilibrium fly population at lower temperatures implies a far greater pupal mass in the ground than at higher temperatures.

Surviving flies (as distinct from pupae) are of no real consequence to the outcome of a spraying operation. It is the daughters of pre-spray-existing pupae, still in the ground at the end of spraying, which constitute the greatest threat to successful control by an aerial spraying operation and not third, or higher, generation pupae. Current strategies suggest that the population is marginally more vulnerable at around 16°C (although compliance with conventional strategy involves two more sprays than at 22°C). The flies themselves are demonstrated to be at their most vulnerable at around 22°C. The additional effectiveness (at both temperatures) can largely be attributed to the number of required sprays being borderline.

Shell fisheries and other crustacean related enterprises probably need to be protected from insecticide, as do bee hives. A decisive emergency-response strategy to implement precautions and clean-up operations in the event of unforeseen accidents (e.g. spillages and flight emergencies) needs to be formulated.

## 9 Acknowledgements

This work was carried out mostly under the supervision of John Hargrove. Abdalla Latif and the Onderstepoort Veterinary Institute are thanked for their generosity in co-funding this work.

## References

- [1] J. W. Hargrove. Age-dependent changes in the probabilities of survival and capture of the tsetse, *glossina morsitans morsitans* westwood. *Insect Science and its Applications*, 11(3):323–330, 1990.
- [2] J. W. Hargrove. Age dependent sampling biases in tsetse flies (*glossina*). problems associated with estimating mortality from sample age distributions. *Management of Insect Pests: Nuclear and Related Molecular and Genetic Techniques* \*\*\*pp. International Atomic Energy Agency, Vienna., pages 549–556, 1993.
- [3] J. W. Hargrove. Reproductive rates of tsetse flies in the field in Zimbabwe. *Physiological Entomology*, 19:307–318, 1994.
- [4] J. W. Hargrove. Towards a general rule for estimating the day of pregnancy of field caught tsetse flies. *Physiological Entomology*, 20:213–223, 1995.
- [5] J. W. Hargrove. Tsetse eradication; sufficiency, necessity and desirability. Technical report, DFID Animal Health Programme, Centre for Tropical Veterinary Medicine, University of Edinburgh, 2003.
- [6] J. W. Hargrove. *Tsetse population dynamics*. Editors: I. Maudlin, P. H. Holmes and P. H. Miles. CABI publishing, Oxford, U.K., 2004.

- [7] B. S. Hursey and R. Allsopp. Sequential applications of low dosage aerosols from fixed wing aircraft as a means of eradicating tsetse flies (*Glossina* spp) from rugged terrain in Zimbabwe. Technical report, Harare, Tsetse and Trypanosomiasis Control Branch, 1983.
- [8] B. S. Hursey and R. Allsopp. The eradication of tsetse flies (*Glossina* spp) from western Zimbabwe by integrated aerial and ground spraying. Technical report, Harare, Tsetse and Trypanosomiasis Control Branch, 1984.
- [9] P. M. Kgori, S. Modo, and S. J. Torr. The use of aerial spraying to eliminate tsetse from the Okavango Delta of Botswana. *Acta Tropica*, 99:184–199, 2006.
- [10] S. G. A. Leak. *Tsetse Biology and Ecology*. CABI, 1999.
- [11] P. Nagel. Environmental monitoring of tsetse control operations in Zambia and Zimbabwe. Technical report, Scientific Environmental Monitoring Group (SEMG) Project, 1993.
- [12] J. S. Perkins and Ramberg L. Environmental recovery monitoring of tsetse fly spraying impacts in the Okavango delta – 2003. Technical report, Harry Openheimer Okavango Research Centre, Botswana, 2004.
- [13] R. J. Phelps and P. M. Burrows. Puparial duration in *Glossina morsitans orientalis* under conditions of constant temperature. *Entomologia Experimentalis et Applicata*, 12:33–43, 1969.
- [14] S. E. Randolph, D. J. Rogers, and F. A. S. Kuzoe. Local variation in the population dynamics of *Glossina palpalis palpalis* (robineau-desvoidy) (Diptera: Glossinidae). ii. the effect of insecticidal spray programmes. *Bulletin of Entomological Research*, 74:425–438, 1984.
- [15] D. A. Turner and R. Brightwell. An evaluation of a sequential aerial spraying operation against *Glossina pallidipes* Austen (Diptera: Glossinidae) in the Lambwe Valley of Kenya: aspects of the post-spray recovery and evidence of natural population regulation. *Bulletin of Entomological Research*, 76:331–349, 1986.
- [16] Brian G. Williams, Robert D. Dransfield, and Robert Brightwell. Tsetse fly (diptera: Glossinidae) population dynamics and the estimation of mortality rates from life-table data. *Bulletin of Entomological Research*, 80:479–485, 1990.

